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Maurer, Urs ; Brem, Silvia ; Liechti, Martina ; Maurizio, Stefano ; Michels, Lars ; Brandeis, Daniel

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Frontal Midline Theta Reflects Individual Task Performance in a Working Memory Task

Urs Maurer · Silvia Brem · Martina Liechti ·
Stefano Maurizio · Lars Michels · Daniel Brandeis

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Abstract Frontal midline (fm-)theta activity has been related to working memory (WM) processes, as it typically increases with WM load. The robustness of this effect, however, varies across studies and subjects, putting limits to its interpretation. We hypothesized that variation in the fm-theta effect may reflect individual differences in task difficulty with increasing WM load as indicated by behavioural responses. We further tested whether effects in the alpha range are robust markers of WM load. We recorded 64-channel EEG from 24 healthy adults while they memorized either 2 or 4 unfamiliar symbols (low vs. high WM load) in a modified Sternberg task. The last 2 s of the retention phase were analyzed for WM load-related changes in the theta (5–7 Hz) and alpha range (lower: 8–10 Hz, upper: 10.5–12.5 Hz). Higher WM load led to less accurate and slower responses. The increase of fm-theta with WM load was most pronounced at fm electrodes, localized to anterior cingulate regions, and correlated with the participants' decrease in accuracy due to higher WM load. Alpha peak frequency increased in the high compared

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Keywords Working memory · EEG · Frequency · Theta · Alpha · Individual differences

Introduction

Cognitive processing in humans relies on a working memory (WM) system that allows us to temporarily store and manipulate information (Baddeley 2003). WM dysfunctions are also common in neurological disorders and mental retardation, and are among the most prominent cognitive deficits in psychiatric disorders, such as attention-deficit/hyperactivity disorder (ADHD; Willcutt et al. 2005; Rhodes et al. 2012) or schizophrenia (Lett et al. 2013). WM functions also undergo considerable changes

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U. Maurer (✉)
Department of Psychology, University of Zurich,
Binzmühlestrasse 14/4, CH-8050 Zurich, Switzerland
e-mail: urs.maurer@psychologie.uzh.ch

U. Maurer · S. Brem · D. Brandeis
Neuroscience Center Zurich, University of Zurich and ETH
Zurich, Zurich, Switzerland

S. Brem · M. Liechti · S. Maurizio · D. Brandeis
Department of Child and Adolescent Psychiatry, University of
Zurich, Zurich, Switzerland

L. Michels
Institute of Neuroradiology, University Hospital Zurich, Zurich,
Switzerland

D. Brandeis
Zurich Center for Integrative Human Physiology (ZIHP),
Zurich, Switzerland

D. Brandeis
Department of Child and Adolescent Psychiatry and
Psychotherapy, Central Institute of Mental Health, Medical
Faculty Mannheim/Heidelberg University, Mannheim, Germany

throughout the lifespan, and particularly during development (Best and Miller 2010; Sander et al. 2012), where prominent changes beyond childhood reflect late maturation in adolescence (Dumontheil et al. 2011; van Ewijk et al. 2013). WM dysfunctions are also at least partly amenable to training (Klingberg 2010; but see also Sonuga-Barke et al. 2013). Understanding the neurophysiology of individual differences in WM functions may thus have considerable clinical implications.

Functional magnetic resonance imaging (fMRI) studies suggested that prefrontal regions are associated with executive, and posterior regions with storage processes of WM (Braver et al. 1997; Cohen et al. 1997). However, time-sensitive techniques, such as Electro- or Magnetoencephalography (EEG/MEG), are needed to reliably separate different processing steps. In a seminal study, Gevins et al. (1997) demonstrated that frontal midline (fm-)theta oscillations of the EEG which characterize a wide range of mental tasks (Ishihara and Yoshi 1972) specifically increased with WM load in an n-back task and could be localized to anterior cingulate regions, a region shown to be activated during attention-demanding tasks (Ishii et al. 1999). But because each n-back stimulus also required a decision, the effects could not be assigned to the maintenance phase of WM processing only.

Isolating the maintenance phase is possible in Sternberg-type tasks in which stimulus, retention, and probe are temporally separated (Sternberg 1966). Accordingly, Jensen and Tesche (2002) demonstrated in an MEG study that theta indeed increased with WM load during retention. Not only in visual associative WM tasks (Boonstra et al. 2013) but also during a Sternberg WM task, Meltzer et al. (2007) and Michels et al. (2008) localized the fm-theta increase during retention to frontal and anterior cingulate regions, i.e. in regions which are involved in behavioral monitoring (Luu et al. 2004) and valuation of response outcomes. Based on animal studies and human data it has been suggested that prefrontal theta oscillations during WM maintenance could reflect prefrontal-hippocampal communication, e.g. to promote successful memory encoding and to induce long-term potentiation and learning (Benchenane et al. 2010), as well as a physiological mechanism to segregate and select information maintained in WM (Benchenane et al. 2011; Sauseng et al. 2010).

In the study by Michels et al. (2008), however, a WM-dependent fm-theta increase was absent in more than 20 % of the subjects, confirming that these effects are highly variable (Jensen et al. 2002). Large individual variability puts limits to the interpretation of fm-theta effects and to their use for research on WM processes. Especially, as it could be recently shown that coherence (rather than amplitude) increased between fm-theta and temporal-parietal sites with increasing memory load (Payne and Kounios 2009).

Given the relation between behavioural responses and other EEG frequencies at the individual level (e.g., alpha rhythm; Surwillo 1961; Klimesch 1999), the aim of the present study was to test whether differences in task performance would correspond to individual differences in the increase of fm-theta due to increased WM load. In accordance with the general direction of the WM load effect we hypothesized that participants, who experience the WM load increase as more demanding (indicated by lower accuracy or slower reaction time), also show a larger theta increase. To test this hypothesis we presented a similar Sternberg-type task as in Michels et al. (2010), but used unfamiliar, nonverbal (visual-figural) stimuli in order to minimize verbal strategies and increase individual variability in task performance. As previous EEG studies showed maximal theta WM load effects in the fm scalp region we focussed on the channel in this region (AFz), but also applied a mapping approach to remain sensitive to different topographies reflecting different source configurations (for an overview see: Michel et al. 2009).

We further investigated WM load-related changes in the alpha range. Previous studies did not agree whether increasing WM load would lead to an alpha decrease (Gevins et al. 1997), to an increase (Scheeringa et al. 2009; Jensen et al. 2002; Boonstra et al. 2013), or whether the direction of change differed between individuals (Michels et al. 2008; Meltzer et al. 2007). Based on a previous study (Michels et al. 2008) we expected a decrease in lower alpha, but an increase in upper alpha, reflected by an overall shift of the alpha peak towards higher frequencies with increasing WM load (Klimesch et al. 2007), which might reconcile the differing results.

Methods

Subjects

Participants were 24 adults (18 females) between 21 and 30 years old (mean age: 24.6 years) and were right-handed (except for 2 left-handed subjects). They reported normal or corrected-to-normal vision and the absence of any neurological or psychiatric disorders. They provided informed consent according to a protocol approved by the local Ethics Committee.

Procedure

In a modified Sternberg task (Fig. 1, similar to: Jensen and Tesche 2002; Michels et al. 2010, 2008) 80 trials (40 per condition) were presented, each consisting of the sequential presentation of a stimulus slide (duration 2.5 s), a retention slide (duration 3.5 s), a probe slide (duration 0.5 s), and a fixation cross (random duration between 1.8 and 2.5 s).

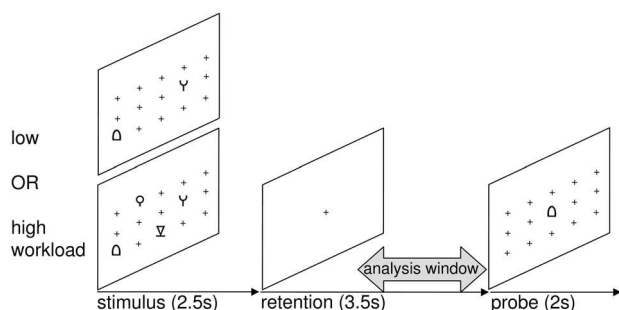


Fig. 1 In a modified Sternberg task the participants saw either 2 or 4 unfamiliar symbols (low vs. high WM load) for 2.5 s. They needed to retain the symbols in WM for 3.5 s, when the symbols were replaced by a fixation cross, and decide whether one of the symbols matched a probe symbol shown at the end of the trial

The stimulus slide consisted of a rectangular grid of 15 crosses (grid: 5.3×3.1 degrees of visual angle; one cross: 0.5×0.5 degrees) that were randomly replaced by either 2 (low WM load) or 4 (high WM load) unfamiliar, nonverbal symbols (from a set of 14, with a size of 0.6×0.9 degrees each). The probe slide consisted of the same grid of crosses with the probe symbol being presented always in the middle. The probe requested a Yes/No response depending on whether the symbol was part of the stimulus set or not.

Behavioral Analysis

Percent correct and reaction time was computed for the responses in the low and high WM load condition, and the differences between the conditions were tested using *t*-tests. In order to correlate accuracy and reaction time data with the EEG data, the differences between the high and low WM load conditions were computed (WM load effect = $L4 - L2$).

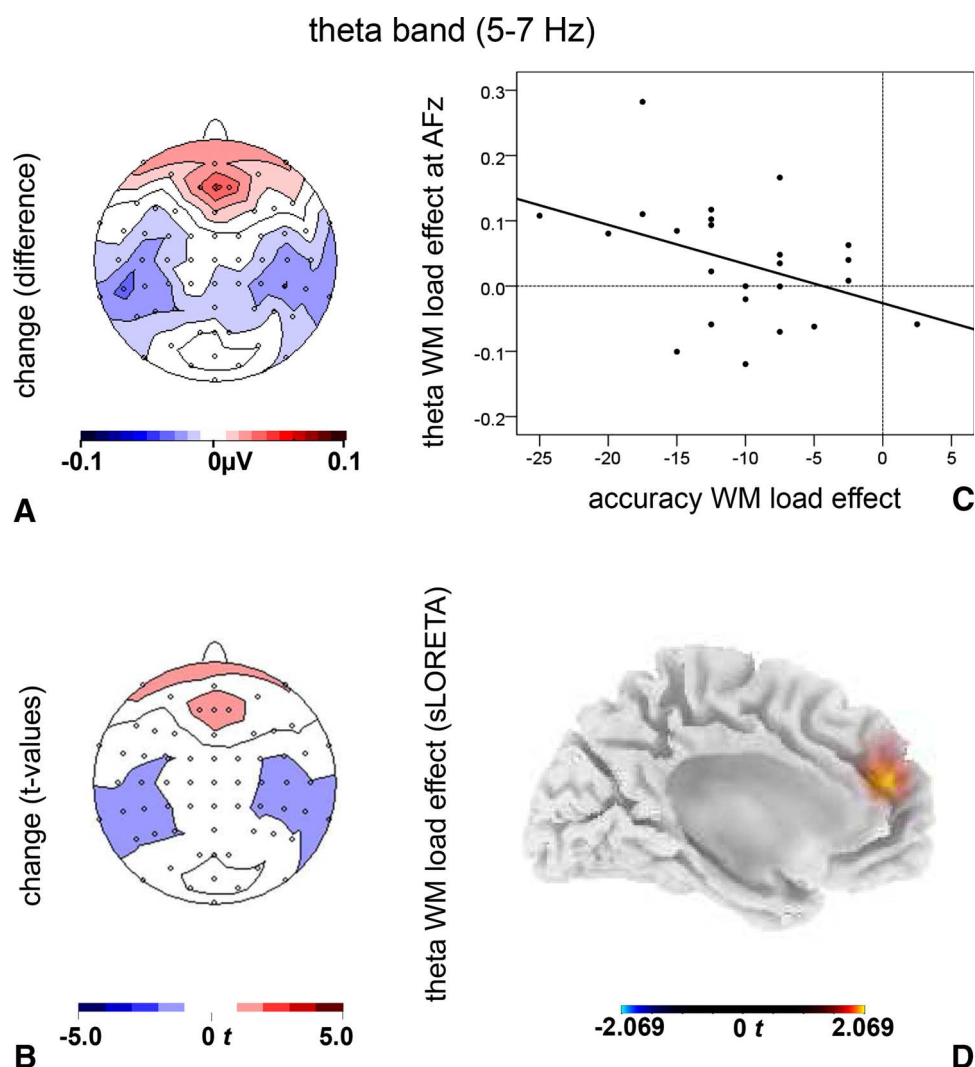
EEG Recording and Analysis

64 electrodes were positioned using elastic caps (FMS, Munich) that included all 10–20 positions plus additional electrodes: Fpz, AFz, FCz, CPz, POz, Oz, Iz, AF1/2, F5/6, FC1/2/3/4/5/6, FT7/8/9/10, C1/2/5/6, CP1/2/3/4/5/6, TP7/8/9/10, P5/6, PO1/2/9/10 and OI1/2. Electrodes O1'/2' and Fp1'/2' were placed 2 cm more laterally for more even coverage (as in: Maurer et al. 2007; Schulz et al. 2008). During the task the EEG was recorded at 500 Hz/channel using Quickamps amplifiers (high pass filters: DC; low pass filters: 70 Hz; average reference), except for 6 subjects who were recorded using Synamps amplifiers with the same settings, but an Fz recording reference. As the different amplifiers did not affect the WM load effects, the data were collapsed for this study. Data were downsampled to 256 Hz,

bandpass-filtered (0.1–70 Hz), and re-referenced to an Fz reference (for Quickamps recordings only) before correcting for horizontal and vertical (blinks) eye movements (Jung et al. 2000). All data were re-referenced to the average reference (Lehmann and Skrandies 1980) for further data processing and analysis. The EEG was segmented to include the last 2 s (i.e., 512 data points) during the retention interval before the occurrence of the probe. Only segments from correct trials and without any residual artefacts (maximal allowed difference: $100 \mu\text{V}$ for eye electrodes, $200 \mu\text{V}$ for the remaining electrodes) were used. For each of these segments a Fast Fourier Transformation was computed (Hanning window: 10 %), and the resulting Power Density values (resolution of 0.5 Hz) were averaged across segments, separately for the low and high WM load conditions. The average power density across all channels was computed separately for each condition and subject. Mean bands were computed for theta (5–7 Hz) and for lower (8–10 Hz) and upper (10.5–12.5 Hz) alpha frequencies at the individual level. Given the intrinsically skewed distribution of power spectra (i.e., obtained through squaring), the averaged power values in each band were log transformed, which has been shown to result in approximately normal distributions of power spectra across subjects (Gasser et al. 1982). The WM load effect in each of the 3 bands was computed as the difference between the log-transformed power values of the high and the low WM load conditions (WM load effect = $\log(L4) - \log(L2)$) and tested using *t*-tests ($\log(L4)$ vs. $\log(L2)$) for the average across all channels. Maps showing WM load effects and the corresponding *t*-values are illustrated for each band. WM load differences between bands were further tested using an ANOVA on the average of the log-transformed power values with the within subject factors “load” ($L4$ vs. $L2$) and “band” (theta vs. lower alpha vs. upper alpha). Given that previous studies had shown maximal theta WM load effects at fm electrodes (Michels et al. 2008; Gevins et al. 1997), we also tested the WM load effect in the theta band at electrode AFz ($\log(L4)$ vs. $\log(L2)$). In order to test the relation between behavioural responses and the theta WM load effect, Pearson correlations were computed between the WM load effect at AFz ($\log(L4) - \log(L2)$) and the WM load effect in accuracy and reaction time. Sources of the WM load effects were estimated using sLORETA (Pascual-Marqui et al. 1999). The filtered (0.1–70 Hz) and the segmented EEG data (correct trials only) of each subject were transformed into cross-spectra values, averaged for each frequency band, and transformed into sLORETA current density values. After log-transformation the sLORETA current density values were compared between the high and the low WM load condition for each band using voxel-wise *t* tests (two-tailed).

In addition, peak frequency in the alpha band (8–12.5 Hz) was identified in the average across all

Fig. 2 Theta (5–7 Hz, log-transformed) increased during the last 2 s of the retention phase in the high WM load condition compared to the low WM load condition most prominently at fm electrodes (a), where t -values testing increase also tended to be significant (c). The sources of the theta increase were estimated (sLORETA) to be located in medial frontal regions extending into anterior cingulate and superior frontal areas (MNI coordinates in Supplementary Table 1). In addition, a theta decrease was located in superior frontal, as well as in inferior parietal and superior temporal regions (Supplementary Table 1 and Supplementary Fig. 2). The WM load-related increase of fm-theta (at AFz) was significantly correlated with the WM load-related decrease in accuracy ($r = -0.41$, $p < 0.05$; b)



channels in each subject for the high and low WM load condition separately, and tested using a t test. The difference of this peak between the two WM load conditions (L4–L2) was used for correlations with behavioural measures.

Results

Behavioural Results

The participants were less accurate and slower in the high WM load compared to the low WM load condition (83.6 % [± 6.3 SD] vs. 94.1 % [± 3.1 SD], $t = -8.2$, $p < 0.001$; 1,118 ms [± 188 SD] vs. 979 ms [± 188 SD], $t = 7.1$, $p < 0.001$).

EEG Results

Theta effects. The high WM load condition tended to elicit increased theta power (log-transformed) at electrode AFz

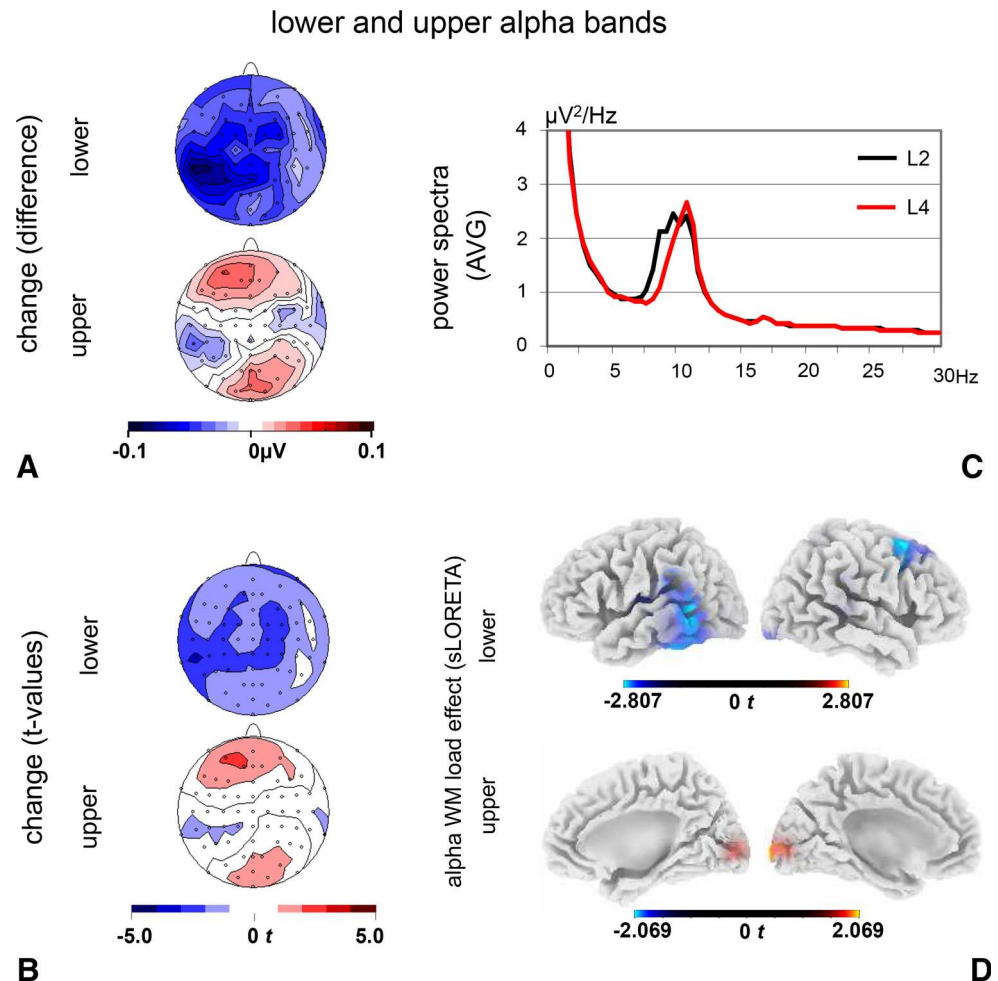
(-0.03 vs. -0.07 ; $t[23] = 1.92$, $p < 0.1$; see also Fig. 2a, b), but not for the average across all channels (-0.13 vs. -0.12 ; $t[23] = -0.59$, $p = \text{ns}$) compared to the low WM load condition, indicating considerable interindividual variance at the fm channel in agreement with previous studies (Jensen and Tesche 2002; Michels et al. 2008).

sLORETA showed increased theta activity in the anterior cingulate cortex (Fig. 2d) and decreased theta activity in left parietal and right superior frontal regions (Supplementary Fig. 2). The theta increase at AFz (difference of log-transformed power) correlated significantly with accuracy difference ($r = -0.41$, $p < 0.05$; Fig. 2c), indicating larger theta increase with larger accuracy decrease (Fig. 2). It was, however, not significantly correlated with reaction time difference ($r = -0.14$, $p = \text{ns}$).

Alpha Effects

The high WM load condition elicited less alpha power across all channels in the lower band compared to the low

Fig. 3 Higher WM load induced a power decrease in the lower alpha band across the entire map compared to lower WM load (log-transformed; **a**), which was most significant at a left temporal electrode (TP7: $t(23) = -3.35$, $p < 0.01$; **b**), in agreement with left temporal sources (**d**; see details in Supplementary Table 2). Higher WM load also led to an increase in upper alpha at frontal and occipital channels (both; **a**), reaching significance at frontal channels and localizing to medial occipital regions (**d**; see details in Supplementary Table 3). The alpha peak in the average across all channels (AVG) occurred at higher frequencies in the high compared to the low WM load condition (**c**)



WM load condition (-0.03 vs. 0.02 , $t[23] = -2.09$, $p < 0.05$; Fig. 3a, b). The corresponding increase for the upper alpha band, however, was not significant (-0.01 vs. -0.02 ; $t[23] = 0.37$, $p = ns$; Fig. 3a, b). The alpha decrease in the lower band with higher WM load was also reflected by a shift of the (overall) alpha peak towards higher frequencies with higher WM load (mean: 10.4 vs. 10.0 Hz, $t[23] = -3.5$, $p < 0.01$; Fig. 3c). The WM load-dependent shift of the alpha peak was not significantly correlated with neither accuracy difference ($r = 0.27$) nor with reaction time difference ($r = -0.17$). sLORETA showed a robust WM load-related reduction of lower alpha activity in left temporal and right superior frontal regions and a weak increase of upper alpha activity in medial occipital regions.

Discussion

At the group level, an increase of fm-theta with increasing load has been found in most previous WM studies using EEG or MEG (Gevins et al. 1997; Michels et al. 2008;

Jensen and Tesche 2002; Onton et al. 2005; Raghavachari et al. 2001; Gevins and Smith 2000). Some studies, however, also reported the absence of the WM load effect in some subjects (Michels et al. 2008; Jensen et al. 2002). The question about the nature of these individual differences is important, given the prominent role of WM in some clinical disorders (Lett et al. 2013; Willcutt et al. 2005). While replicating the general WM load effect as a trend towards an increase of fm-theta at the group level, we demonstrate here, that such individual differences in this effect can be partly explained by the behavioural task performance.

Specifically, the increase of the fm-theta was larger, the less accurate a participant performed in the difficult compared to the easy condition. Thus, the direction is the same as for the general WM load effect comparing the difficult (high WM load) to the easy (low WM load) condition at the group level. This correlation was not due to the larger number of excluded trials in the subjects with lower accuracy, as a reanalysis of the data using all trials irrespective of response accuracy revealed an even larger correlation of the same direction ($r = -0.50$, $p < 0.05$). We thus believe that the accuracy decrease reflects

individual task difficulty with an increase in WM load and further qualifies the individual effects of a WM load manipulation. We suggest that the reliability of the increase of fm theta as a marker of WM processing may improve, if task performance is included in the analysis. Although the decrease in accuracy was paralleled by response slowing with higher WM load in our study, the correlation between theta increase and behavioural measures was only significant for accuracy. It remains to be investigated in future studies whether in tasks with accuracy performance at ceiling in high WM load conditions, similar correlations can be found with reaction time instead.

The fm-theta WM load effect has been shown to appear in a narrow frequency band (5–7 Hz) in previous studies (Gevins et al. 1997; Michels et al. 2008; Onton et al. 2005), rather than spanning the entire theta band. Still a reanalysis of the present data using the entire 4–7.5 Hz theta band confirmed our WM load effects and behavioural correlations, although the statistical effects became less robust (not reported).

Moreover, the fm-theta WM load effect showed a very focal topography, as it was restricted to a few fm electrodes, similar to previous studies (Gevins et al. 1997; Michels et al. 2008). This characteristic topography resulted in anterior cingulate sources, corroborating earlier source localization attempts (Gevins et al. 1997; Michels et al. 2008). This finding is in agreement with intracranial recordings from epileptic patients during WM tasks which found prominent load-related increases in fm regions (Meltzer et al. 2008), although theta activity during WM processing could be found in many areas throughout the cortex (Raghavachari et al. 2006), which could also reflect alpha activity slowing by antiepileptic medication.

Involvement of anterior cingulate regions in WM processes has also been suggested by fMRI studies, although activation in this region actually decreased with parametrically increasing WM load (Braver et al. 1997), in contrast to the increase in bilateral dorsolateral prefrontal and left inferior frontal regions (Braver et al. 1997; Cohen et al. 1997). This divergence in the same region between theta increase and BOLD decrease with increasing WM load, has been confirmed in more recent simultaneous EEG-fMRI studies showing that theta increase during WM tasks correlated negatively with the BOLD response in medial prefrontal and anterior cingulate regions (Meltzer et al. 2007; Michels et al. 2010; Scheeringa et al. 2009).

In the context of WM theories it is generally assumed that the central executive component is sub-served by frontal cortex functions, whereas storage functions are implemented in posterior brain regions (Baddeley 2003). An increase of fm-theta putatively from anterior cingulate sources thus may indicate an increasing demand of executive control if WM load increases or if task difficulty

increases for a particular individual. Such control mechanisms may be needed either to organize representations of multiple items or to integrate various cognitive sub-processes in WM (Sauseng et al. 2010). Fm-theta and its relation to executive control (Cavanagh et al. 2013), however, may not only be influenced by load and difficulty, but also by expertise. This has been shown in a study by Doppelmayr et al. (2008), in which experts showed increased fm-theta compared with novices in the pre-shot phase during rifle shooting. This may suggest that experts know more aspects of the task at hand that need to be controlled for compared with novices, which increases the demand for executive control. Similarly, the increased theta synchronisation in a modified RAVEN task in subjects with high compared to those with average intelligence (Doppelmayr et al. 2005) may reflect that highly intelligent subjects control more aspects of this intelligence test. However, such effects may be task dependent, and in the context of the present study expertise is supposed to have played a minor role, because all subjects were equally unfamiliar with the stimuli and task.

Similarly, a recent study (Itthipuripat et al. 2013) reported increased theta power in trials that could be manipulated successfully compared to unsuccessfully manipulated trials. This may be due to a larger degree of executive control in the successful trials, whereas engagement of executive control to a lesser degree may have led to unsuccessful task manipulations. Importantly, our findings derive from trials which were always correct, and the number of incorrect trials in our data was too low to compare correct and incorrect trials. Moreover, theta increase may not be linked to behavioural success per se, as increased theta activation could be observed under more difficult conditions, without necessarily affecting behaviour (Park et al. 2013).

In a recent study, Langer et al. (2013) could demonstrate that WM training was uniquely linked to theta power increase during the resting eyes-closed state. The rather widespread distribution of these theta effects on the scalp may suggest that these effects are not just due to an increase of fm theta, and also reflect other sources. Still, WM training may be associated with enhanced executive functions in general and thereby with increased fm theta at rest (Langer et al. 2013).

Although fm-theta seems to play an important role for WM processing as indicated by this and by previous studies, the fm-theta increase reached only the level of a statistical trend at a few frontal electrodes and could not be detected across the average of all electrodes. In contrast, a prominent WM load-related decrease was found for the lower alpha range in the average across all electrodes.

The alpha peak shifted upward with higher WM load resulting in a decrease in the lower alpha range and a (non-

significant) increase in the higher alpha range. Task-specific modulation in the alpha band was first reported by Jensen et al. (2002) showing an alpha increase with higher WM load. Subsequent studies reported either an overall increase with higher WM load (Scheeringa et al. 2009; Jensen et al. 2002) or a subject-specific modulation with an increase in some subjects, but a decrease in other subjects (Meltzer et al. 2007; Michels et al. 2008) - the decrease being most prominent in the lower alpha range (Michels et al. 2008).

Moreover, some of the diverging results may also be driven by outlier values in small groups. In our analysis we used log-transformed values that are more robust against the influence of extreme cases. The same analysis, however, also led to a significant increase of upper alpha (see Supplementary Fig. 1) without log-transformation but with percent change $((L4-L2)/L2*100)$ as in Michels et al. (2008) and Jensen et al. (2002).

The functional significance of alpha activity during WM processing has been related to active inhibition of occipitoparietal areas (Jensen et al. 2002; Klimesch et al. 2007) through top-down control (Klimesch et al. 2007) extending the cortical idling theory of alpha rhythms during rest (Pfurtscheller et al. 1996). Accordingly, alpha would indirectly support retention of visual material, by suppressing processing of distracting visual information. A more active role of alpha for retention (Jensen et al. 2002), however, cannot be excluded and warrants further research.

In summary, the present study corroborates that both theta and alpha rhythms play an important role for WM processes, and extends these findings by demonstrating that fm-theta increase with higher WM load is associated with individual task difficulty indexed by accuracy and that lower alpha decreases with higher WM load corresponding to a shift of the alpha peak towards higher frequencies within the alpha band. Future work should further clarify the clinical significance and the plasticity of these separable WM processes.

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References

- Baddeley A (2003) Working memory: looking back and looking forward. *Nat Rev Neurosci* 4(10):829–839
- Benchenane K, Peyrache A, Khamassi M, Tierney PL, Gioanni Y, Battaglia FP, Wiener SI (2010) Coherent theta oscillations and reorganization of spike timing in the hippocampal–prefrontal network upon learning. *Neuron* 66(6):921–936
- Benchenane K, Tiesinga PH, Battaglia FP (2011) Oscillations in the prefrontal cortex: a gateway to memory and attention. *Curr Opin Neurobiol* 21(3):475–485
- Best JR, Miller PH (2010) A developmental perspective on executive function. *Child Dev* 81(6):1641–1660
- Boonstra TW, Powell TY, Mehrkanoon S, Breakspear M (2013) Effects of mnemonic load on cortical activity during visual working memory: linking ongoing brain activity with evoked responses. *Int J Psychophysiol* 89(3):409–418
- Braver TS, Cohen JD, Nystrom LE, Jonides J, Smith EE, Noll DC (1997) A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* 5(1):49–62
- Cavanagh JF, Eisenberg I, Guitart-Masip M, Huys Q, Frank MJ (2013) Frontal theta overrides pavlovian learning biases. *J Neurosci* 33(19):8541–8548
- Cohen JD, Perlstein WM, Braver TS, Nystrom LE, Noll DC, Jonides J, Smith EE (1997) Temporal dynamics of brain activation during a working memory task. *Nature* 386(6625):604–608
- Doppelmayr M, Klimesch W, Sauseng P, Hodlmoser K, Stadler W, Hanslmayr S (2005) Intelligence related differences in EEG-bandpower. *Neurosci Lett* 381(3):309–313
- Doppelmayr M, Finkenzeller T, Sauseng P (2008) Frontal midline theta in the pre-shot phase of rifle shooting: differences between experts and novices. *Neuropsychologia* 46(5):1463–1467
- Dumontheil I, Roggeman C, Ziermans T, Peyrard-Janvid M, Matsson H, Kere J, Klingberg T (2011) Influence of the COMT genotype on working memory and brain activity changes during development. *Biol Psychiatry* 70(3):222–229
- Gasser T, Bacher P, Mocks J (1982) Transformations towards the normal distribution of broad band spectral parameters of the EEG. *Electroencephalogr Clin Neurophysiol* 53(1):119–124
- Gevens A, Smith ME (2000) Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. *Cereb Cortex* 10(9):829–839
- Gevens A, Smith ME, McEvoy L, Yu D (1997) High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cereb Cortex* 7(4):374–385
- Ishihara T, Yoshi N (1972) Multivariate analytic study of EEG and mental activity in juvenile delinquents. *Electroencephalogr Clin Neurophysiol* 33(1):71–80
- Ishii R, Shinosaki K, Ukai S, Inouye T, Ishihara T, Yoshimine T, Hirabuki N, Asada H, Kihara T, Robinson SE, Takeda M (1999) Medial prefrontal cortex generates frontal midline theta rhythm. *Neuroreport* 10(4):675–679
- Itthipuripat S, Wessel JR, Aron AR (2013) Frontal theta is a signature of successful working memory manipulation. *Exp Brain Res* 224(2):255–262
- Jensen O, Tesche CD (2002) Frontal theta activity in humans increases with memory load in a working memory task. *Eur J Neurosci* 15(8):1395–1399
- Jensen O, Gelfand J, Kounios J, Lisman JE (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb Cortex* 12(8):877–882
- Jung TP, Makeig S, Westerfield M, Townsend J, Courchesne E, Sejnowski TJ (2000) Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clin Neurophysiol* 111(10):1745–1758
- Klimesch W (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res Brain Res Rev* 29(2–3):169–195
- Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53(1):63–88
- Klingberg T (2010) Training and plasticity of working memory. *Trends Cogn Sci* 14(7):317–324
- Langer N, von Bastian CC, Wirz H, Oberauer K, Jancke L (2013) The effects of working memory training on functional brain network efficiency. *Cortex* 49(9):2424–2438

- Lehmann D, Skrandies W (1980) Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalogr Clin Neurophysiol* 48(6):609–621
- Lett TA, Voineskos AN, Kennedy JL, Levine B, Daskalakis ZJ (2013) Treating working memory deficits in schizophrenia: a review of the neurobiology. *Biol Psychiatry* 75(5):361–370
- Luu P, Tucker DM, Makeig S (2004) Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation. *Clin Neurophysiol* 115(8):1821–1835
- Maurer U, Brem S, Bucher K, Kranz F, Benz R, Steinhausen H-C, Brandeis D (2007) Impaired tuning of a fast occipito-temporal response for print in dyslexic children learning to read. *Brain* 130:3200–3210
- Meltzer JA, Negishi M, Mayes LC, Constable RT (2007) Individual differences in EEG theta and alpha dynamics during working memory correlate with fMRI responses across subjects. *Clin Neurophysiol* 118(11):2419–2436
- Meltzer JA, Zaveri HP, Goncharova II, Distasio MM, Papademetris X, Spencer SS, Spencer DD, Constable RT (2008) Effects of working memory load on oscillatory power in human intracranial EEG. *Cereb Cortex* 18(8):1843–1855
- Michel CM, König T, Brandeis D, Gianotti LRR, Wackermann J (2009) *Electrical neuroimaging*. Cambridge University Press, New York
- Michels L, Moazami-Goudarzi M, Jeanmonod D, Sarnthein J (2008) EEG alpha distinguishes between cuneal and precuneal activation in working memory. *Neuroimage* 40(3):1296–1310
- Michels L, Bucher K, Luchinger R, Klaver P, Martin E, Jeanmonod D, Brandeis D (2010) Simultaneous EEG-fMRI during a working memory task: modulations in low and high frequency bands. *PLoS One* 5(4):e10298
- Onton J, Delorme A, Makeig S (2005) Frontal midline EEG dynamics during working memory. *Neuroimage* 27(2):341–356
- Park JY, Min BK, Jung YC, Pak H, Jeong YH, Kim E (2013) Illumination influences working memory: an EEG study. *Neuroscience* 247:386–394
- Pascual-Marqui RD, Lehmann D, Koenig T, Kochi K, Merlo MC, Hell D, Koukkou M (1999) Low resolution brain electromagnetic tomography (LORETA) functional imaging in acute, neuroleptic-naïve, first-episode, productive schizophrenia. *Psychiatry Res* 90(3):169–179
- Payne L, Kounios J (2009) Coherent oscillatory networks supporting short-term memory retention. *Brain Res* 1247:126–132
- Pfurtscheller G, Stancak A Jr, Neuper C (1996) Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *Int J Psychophysiol* 24(1–2):39–46
- Raghavachari S, Kahana MJ, Rizzuto DS, Caplan JB, Kirschen MP, Bourgeois B, Madsen JR, Lisman JE (2001) Gating of human theta oscillations by a working memory task. *J Neurosci* 21(9):3175–3183
- Raghavachari S, Lisman JE, Tully M, Madsen JR, Bromfield EB, Kahana MJ (2006) Theta oscillations in human cortex during a working-memory task: evidence for local generators. *J Neurophysiol* 95(3):1630–1638
- Rhodes SM, Park J, Seth S, Coghill DR (2012) A comprehensive investigation of memory impairment in attention deficit hyperactivity disorder and oppositional defiant disorder. *J Child Psychol Psychiatry* 53(2):128–137
- Sander MC, Lindenberger U, Werkle-Bergner M (2012) Lifespan age differences in working memory: a two-component framework. *Neurosci Biobehav Rev* 36(9):2007–2033
- Sauseng P, Griesmayr B, Freunberger R, Klimesch W (2010) Control mechanisms in working memory: a possible function of EEG theta oscillations. *Neurosci Biobehav Rev* 34(7):1015–1022
- Scheeringa R, Petersson KM, Oostenveld R, Norris DG, Hagoort P, Bastiaansen MC (2009) Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *Neuroimage* 44(3):1224–1238
- Schulz E, Maurer U, van der Mark S, Bucher K, Brem S, Martin E, Brandeis D (2008) Impaired semantic processing during sentence reading in children with dyslexia: combined fMRI and ERP evidence. *Neuroimage* 41(1):153–168
- Sonuga-Barke EJ, Brandeis D, Cortese S, Daley D, Ferrin M, Holtmann M, Stevenson J, Danckaerts M, van der Oord S, Dopfner M, Dittmann RW, Simonoff E, Zuddas A, Banaschewski T, Buitelaar J, Coghill D, Hollis C, Konofal E, Lecendreux M, Wong IC, Sergeant J (2013) Nonpharmacological interventions for ADHD: systematic review and meta-analyses of randomized controlled trials of dietary and psychological treatments. *Am J Psychiatry* 170(3):275–289
- Sternberg S (1966) High-speed scanning in human memory. *Science* 153(736):652–654
- Surwillo W (1961) Frequency of the alpha rhythm, reaction time and age. *Nature* 191:823–824
- van Ewijk H, Heslenfeld DJ, Luman M, Rommelse NN, Hartman CA, Hoekstra P, Franke B, Buitelaar JK, Oosterlaan J (2013) Visuo-spatial working memory in ADHD patients, unaffected siblings, and healthy controls. *J Atten Disord* [Epub ahead of printing]
- Willcutt EG, Doyle AE, Nigg JT, Faraone SV, Pennington BF (2005) Validity of the executive function theory of attention-deficit/hyperactivity disorder: a meta-analytic review. *Biol Psychiatry* 57(11):1336–1346